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PETER LAKE LIES DEEP IN A MAPLE FOREST NEAR THE WISCONSIN-MICHIGAN border. One day in July 2008 a group of scientists and graduate students led by ecologist Stephen Carpenter of the University of Wisconsin-Madison arrived at the lake with some fish. One by one, they dropped 12 largemouth bass into the water. Then they headed for home, leaving behind sensors that could measure water clarity every five minutes, 24 hours a day.

The scientists repeated the same trip two more times in 2009. Each time they dropped 15 more bass into the water. Months passed. The lake cycled through the seasons. It froze over, thawed out and bloomed again with life. Then, in the summer of 2010, Peter Lake changed dramatically. Before the scientists started their experiment, the lake abounded in fathead minnows, pumpkinseeds and other small fish. Now, however, those once dominant predators were rare, for the most part eaten by the largemouth bass. The few survivors hid in the shallows. Water fleas and other tiny animals that the small fish once devoured were now free to flourish. And because these diminutive animals graze on algae, the lake water became clearer. Two years later the ecosystem remains in its altered state.

Peter Lake's food web has flipped, shifting from a longstanding arrangement to a new one. Carpenter triggered the switchover on purpose, as part of an experiment he is running on the factors that lead to persistent changes in the mix of organisms eating and being eaten by one another. Yet in recent decades food webs across the world have also been flipping, often unexpectedly, on a far greater scale. Jellyfish now dominate the waters off the coast of Namibia. Hungry snails and fungi are overrunning coastal marshes in North Carolina, causing them to disintegrate. In the northwestern Atlantic, lobsters are proliferating while cod have crashed.

Whether by fishing, converting land into farms and cities, or warming the planet, humanity is putting tremendous stresses on the world's ecosystems. As a result, ecologists expect many more food webs to flip in the years ahead. Predicting those sud-

den changes is far from straightforward, however, because food webs can be staggeringly complex.

That is where Carpenter comes in. Taking advantage of 30 years of ecological research at Peter Lake, Carpenter and his colleagues developed mathematical models of ecological networks that allowed them to pick up early-warning signs of the change that was coming, 15 months before its food web flipped. "We could see it a good long ways in advance," Carpenter says.

With the help of such models, he and other scientists are beginning to decipher some of the rules that determine whether a food web will remain stable or cross a threshold and change substantially. They hope to use their knowledge of those rules to monitor the state of ecosystems so that they can identify ones at risk of collapse. Ideally, an early-warning system would tell us when to alter human activities that are pushing an ecosystem toward a breakdown or would even allow us to pull ecosystems back from the brink. Prevention is key, they say, because once ecosystems pass their tipping point, it is remarkably difficult for them to return.

#### MATHEMATICAL PREDATORS

CARPENTER'S WORK builds on a century of basic research by ecologists who have sought to answer a simple question: Why are the populations of different species the way they are? Why, for example, are there so many flies and so few wolves? And why do the sizes of fly populations vary greatly from one year to the next? To find an answer, ecologists began to diagram food webs, noting who ate whom and how much each one ate. Yet food

#### IN BRIEF

**Food webs** are complex, but mathematical models can reveal critical links that, if disturbed, can cause the webs to flip to a different state, including collapse.

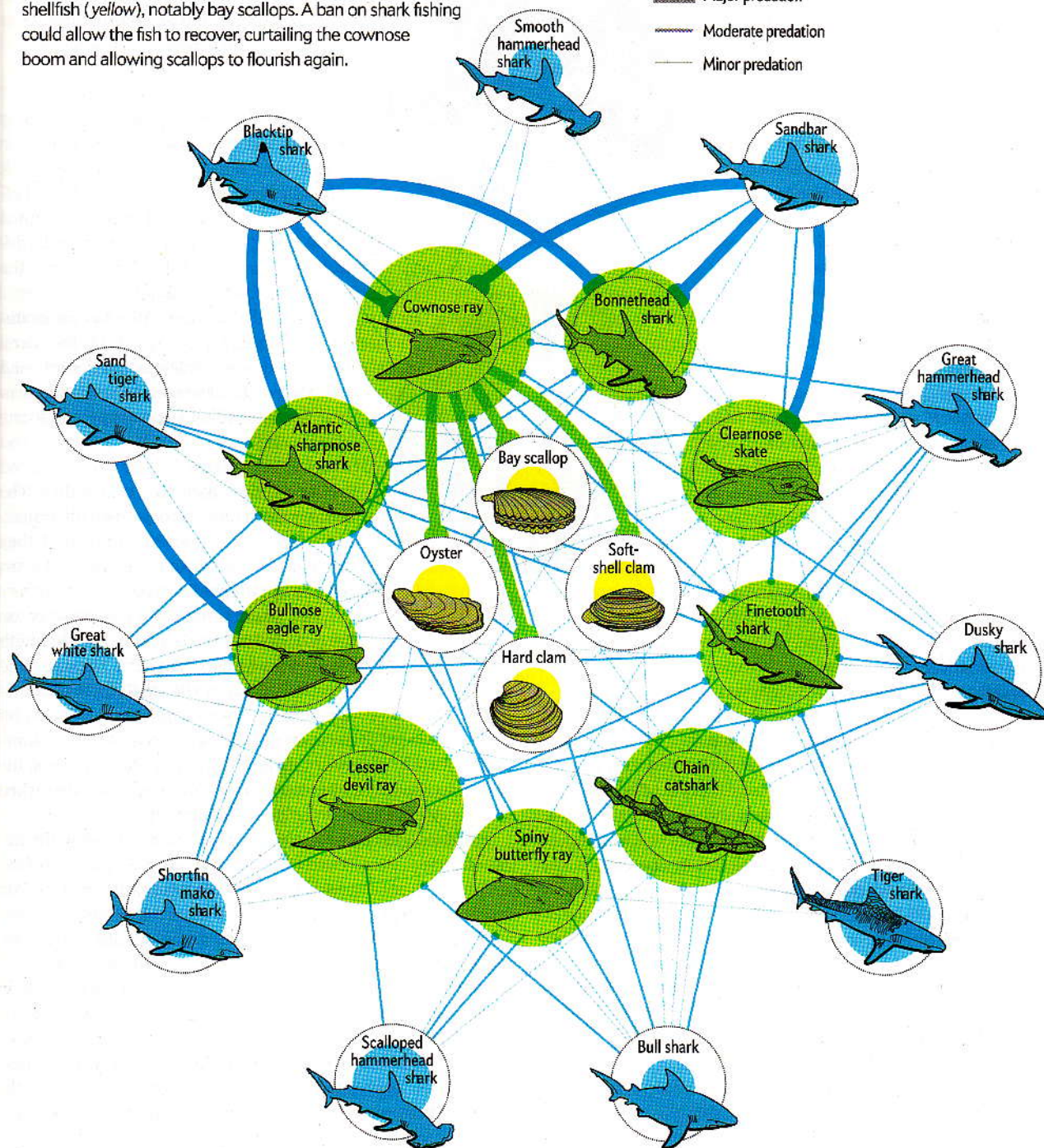
**Once the flipping** of food webs takes place, they are often unlikely to return to their original state. **Experiments** in Peter Lake and Paul Lake near the Mich-

igan-Wisconsin border are showing that models can predict a flip before it occurs, giving ecologists a chance to alter an ecosystem and pull it back from the brink.



# Fewer Sharks, Scallops

After decades of thinking that food webs are structured from the bottom up, researchers are finding that top predators often control the chain—directly and indirectly. A study by Julia Baum, now at the University of Victoria in British Columbia, and others shows that overfishing of large sharks (blue) off the eastern U.S. has allowed midlevel predators (green) to grow in number, especially the cownose ray. The expanded population, in turn, has devastated certain shellfish (yellow), notably bay scallops. A ban on shark fishing could allow the fish to recover, curtailing the cownose boom and allowing scallops to flourish again.





webs can encompass dozens, hundreds or thousands of species; their complexity often turned attempted diagrams into hopeless snarls.

To make sense of the snarls, ecologists have turned food webs into mathematical models. They write an equation for the growth of one species by linking its reproduction rate to how much food it can obtain and how often it gets eaten by other species. Because all those variables can change, solving the equations for even simple food webs has proved overwhelming. Fortunately, the rise of fast, cheap computers has recently allowed ecologists to run simulations of many different kinds of ecosystems.

Out of this work, ecologists discovered some key principles operating in real food webs. Most food webs, for instance, consist of many weak links rather than a few strong ones. Two species are strongly linked if they interact a lot, such as a predator that consistently devours huge numbers of a single prey. Species that are weakly linked interact occasionally: a predator snacks every now and then on various species. Food webs may be dominated by numerous weak links because that arrangement is more stable over the long term. If a predator can eat several species, it can survive the extinction of one of them. And if a predator can move on to another species that is easier to find when a prey species becomes rare, the switch allows the original prey to recover. The weak links may thus keep species from driving one another to extinction. "You see it over and over again," says Kevin McCann, an ecologist at the University of Guelph in Ontario.

Mathematical models have also revealed vulnerable points in food webs, where small changes can lead to big effects throughout entire ecosystems. In the 1960s, for example, theoreticians proposed that predators at the top of a food web exerted a surprising amount of control over the size of populations of other species—including species they did not directly attack. The idea of this top-down control by a small fraction of animals in an ecosystem was greeted with skepticism. It was hard to see how a few top predators could have such a great effect on the rest of their food web.

But then we humans began running unplanned experiments that put this so-called trophic cascade hypothesis to the test. In the ocean, we fished for top predators such as cod on an industrial scale, while on land, we killed off large predators such as wolves. We introduced invasive species such as rats to islands and gave a variety of other shocks to the world's ecosystems. The results of these actions vindicated the key role of predators and the cascading effects they can have from the top of a food web on down.

Ecologists realized that, as predicted, changes in certain pred-



**UNINTENDED CUT:** Removing gray wolves from Yellowstone National Park allowed a boom in elk, which dined on aspen leaves, killing many young trees.

ators had massive impacts on food webs. The slaughter of wolves around Yellowstone National Park led to a boom in elk and other herbivores. The elk feasted on willow and aspen leaves, killing many trees. Likewise, off the eastern U.S. coast, fishers have devastated oyster and scallop populations without catching a single one. Instead they have killed sharks in huge numbers, allowing the smaller predatory fish the sharks fed on to thrive. The population of cownose rays, for example, has exploded. Cownose rays feed on bottom-dwelling shellfish, and as a result, their boom has led to a crash in oysters and scallops.

#### THE STICKY SWITCH

MANY OF THESE FLIPS have taken ecologists by surprise. And they have realized that forecasting when a food web will change drastically is important because once it does, it often sticks; returning a food web to its original state is hard. "Getting back is really, really difficult," says ecologist Villy Christensen of the University of British Columbia.

In the northwestern Atlantic, for example, cod fisheries collapsed in the early 1990s. Cod are voracious predators, and with their disappearance came a boom in their prey, including sprats, capelins, young lobsters and snow crabs. To try to allow cod to recover, managers put strict limits on cod fishing or even banned it altogether. The mathematical models they relied on indicated that if the fish were left unmolested, they would be able to lay enough eggs and grow fast enough to rebuild their population.

"The predictions for recovery were on the order of five to six years," says Kenneth Frank, a research scientist at Fisheries and Oceans Canada at the Bedford Institute of Oceanography who studies cod fisheries off the coast of Nova Scotia and Newfoundland.

The predictions were wrong, however. Even after six years, the cod showed no sign of recovery. Instead the species languished at a few percent of its precollapse population.

Frank and his colleagues have now figured out why: the initial estimates were based only on how fast cod can reproduce, not on how the whole food web is organized. Adult cod feed on sprats and capelins and other prey known collectively as forage fish. The forage fish, in turn, eat tiny animals known as zooplanktons, including the eggs and larvae of cod themselves.

Before cod were overfished, they kept the forage fish in check, so that the small fish could not eat enough eggs and larvae to put a dent in the cod population. Once humans lowered the cod population, though, the tables were turned. The forage fish boomed and could devour a substantial fraction of the young cod. Even without humans fishing them, the cod were unable to rebound.

Only now are Frank and his co-workers seeing signs of a de-



layed recovery. After falling to as low as 1 percent of their precrash levels, the cod have risen in recent years to 30 percent. The key, Frank says, is that the forage fish have exploded to such high numbers that they are outstripping their own food supply and are starting to crash. Now that their population has dropped, cod eggs and larvae have a much better chance to reach adulthood. If cod can return to their former levels, they will be able to keep the populations of forage fish down once more. "That's the trajectory they're on, but there are lots of surprises because these ecosystems are so complex," Frank says.

Food webs will continue to flip around the world. Some will do so because of hunting and fishing, but others will be buffeted by other forces. For example, lionfish, native to the Pacific, became popular as pets in the U.S., but East Coast owners who grew tired of them began dumping them into the Atlantic, where they are now menacing Caribbean coral reefs. They are eating so many small prey species that ecologists predict they will outcompete and drive down many of the native predators, including sharks. Climate change is also altering food webs, in some cases by shifting the ranges of predators and their prey. No matter what the driver of food web changes, they may be able to push the ecosystems over major thresholds. And if those ecosystems have sticky switches, it will be very hard to restore them.

#### EARLY WARNING PREVENTS COLLAPSE

SOME SCIENTISTS SAY that preventing food webs from switching is a more effective strategy than trying to restore ones that have flipped. They believe an ounce of ecological prevention may be worth a pound of cure. Carpenter and his colleagues have been developing an early-warning system that can reveal when ecological switches are about to happen and offer some guidance about how to pull an ecosystem back from the tipping point.

"Ecologists had always thought these things were completely unpredictable," Carpenter says. That is why, eight years ago, he and his colleagues began to create equations that could capture how ecosystems work. They included variables for such factors as the reproduction rate of species and the rate at which different species eat one another. These equations produced ecosystem models that could reach tipping points at which they would suddenly convert into a new state, just as real ecosystems do.

The scientists could also see subtle yet distinctive patterns developing long before the virtual ecosystems abruptly changed—an ecological version of distant rumbles that precede a storm. One pattern that surfaced, for example, was that when an ecosystem was disturbed—say, by a sudden swing in temperature or a disease outbreak—it began to take longer than usual to return to its regular state. "As it gets closer to the tipping point, it recovers more slowly from perturbations," says Marten Scheffer, an ecologist at Wageningen University in the Netherlands who has worked with Carpenter on early-warning systems.

Scheffer, Carpenter and their co-workers are testing their models in a range of experiments. Some have taken place in the carefully controlled confines of laboratories. Carpenter's exper-

**CARPENTER IS DEVELOPING AN EARLY-WARNING SYSTEM THAT CAN REVEAL WHEN A FOOD WEB IS ABOUT TO FLIP AND OFFER GUIDANCE ABOUT HOW TO PULL IT BACK FROM THE BRINK.**

iment in Peter Lake was the first time they had put the early-warning system to a test in a natural ecosystem. Once the scientists started to stock Peter Lake, they performed daily recordings of the zooplanktons, phytoplanktons and fishes in the water. They also monitored nearby Paul Lake, similar in size, which they did not manipulate. Any changes that occurred in both lakes would presumably be the result of external factors in the climate. In the summer of 2009 the scientists began to see rapid rises and falls in the chlorophyll levels in Peter Lake. The lake's jitters matched the patterns that come before an ecosystem flips in Carpenter's models. Paul Lake, meanwhile, showed no such change.

Carpenter and his colleagues hope to develop monitoring systems that can detect similarly telltale fluctuations that foreshad-

ow an imminent change in other ecosystems, from wetlands to forests to oceans. "There are many tricky aspects to it, but it does work," Scheffer says.

The goal, of course, is to know when we are pushing an ecosystem to the brink, so we can stop pushing. To test this idea, Carpenter is manipulating Peter Lake again. Instead of adding top predators, this time he is adding fertilizer, which will likely lead to a boom of algae. That, in turn, will trigger changes throughout the lake's ecosystem. Carpenter expects that a number of bigger fish species—including those largemouth bass—will crash as a result and then remain stuck at low levels. He also expects to get warning signs of this change months in advance, in the form of chlorophyll fluctuations and other subtle patterns. Once he sees those signs, Carpenter will stop supplying the extra fertilizer. If he is right, the ecosystem will return to its normal state instead of flipping. For comparison, he will add fertilizer to nearby Tuesday Lake, but he will not stop when he does at Peter Lake. Paul Lake will again be left untreated, as a control.

Carpenter is optimistic that the early-warning system he is developing will work not just in isolated lakes but in any ecosystem, thanks to the way ecological networks are organized. Yet success would not mean that predicting a flip would be certain. The equations that he and his colleagues have developed suggest that some disturbances will be so dramatic and fast that they will not leave time for ecologists to notice that trouble is coming. "Surprises will continue," Carpenter says, "although the early-warning system does provide the opportunity to anticipate some surprises before they happen." ■

#### MORE TO EXPLORE

Human Involvement in Food Webs. Donald R. Strong and Kenneth T. Frank in *Annual Review of Environment and Resources*, Vol. 35, pages 1-23; November 2010.

Trophic Cascades: Predators, Prey, and the Changing Dynamics of Nature. Edited by John Terborgh and James A. Estes. Island Press, 2010.

Food Webs. Kevin S. McCann. Princeton University Press, 2011.

#### SCIENTIFIC AMERICAN ONLINE

For an interactive graphic showing predator effects on food webs in the Adriatic Sea, go to [ScientificAmerican.com/oct2012/zimmer](http://ScientificAmerican.com/oct2012/zimmer)